Short-term foraging dynamics of cattle grazing swards with different canopy structures[1]

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ABSTRACT: The objective of the present experiment was to describe the sward canopy structures of 3 different wheat (*Triticum aestivum* L.) pastures and relate them to short-term herbage intake rate and foraging dynamics by steers. Pastures were sampled for leaf and stem fractions at the bottom, middle, and top canopy strata. Sward surface heights and tiller and bulk densities were measured. Herbage was separated into stem and leaf, and leaves were then ranked phenologically. Three steers grazed (grazing sessions) 3 different pastures in a Latin square design. Ruminal contents were emptied and weighed before and after grazing sessions to assess herbage intake rate and bite mass. All grazing sessions were video recorded and analyzed for feeding stations (eating steps demarking the potential area of herbage consumption), bites per feeding station, and feeding stations per minute. Bite depth, bite area, and area grazed per feeding station were calculated. Morphological components and tiller density did not differ ($P > 0.05$) between the pastures, but sward surface height ($P < 0.05$) and leaf proportions in the middle and top canopy strata did differ. The herbage intake rate, bite mass, and bite area differed between treatments ($P < 0.05$). Steers grazing the tallest pasture with the greatest leaf accessibility ate faster, navigated slower, and grazed more efficiently ($P < 0.05$). The area grazed per feeding station differed between treatments ($P < 0.05$), being 87% for the tallest pasture with the greatest leaf accessibility and the least, 31%, for the pasture with the least leaf accessibility. Pastures with greater leaf accessibility may lead grazing cattle to reach the same herbage intake amount in less time while grazing more efficiently per unit area. Therefore, it may be logical to reduce the area and time allocations in pastures with taller swards where a leafy upper canopy stratum is found.

Key words: behavior, herbage intake, steer, sward structure

J. Anim. Sci. 2009. 87:3817–3824
doi:10.2527/jas.2009-2094

INTRODUCTION

Herbage intake is a key determinant of cattle performance in pasture-based production systems (Kolver and Muller, 1998). Herbage intake depends not only on herbage nutritive value, but also on its availability (Hirata, 2002) and accessibility (Ungar and Noy-Meir, 1988), with the latter being directly related to sward canopy structure. Most advances in the appreciation of the plant-animal interface have come from research based on either artificially modified or constructed swards (Laca et al., 2001). At best, such studies can

[1]The project was conducted with funding from the University of Arkansas Agricultural Experiment Station, Hatch Project AR001735, and the National Research Initiative of the USDA Cooperative State Research, Education, and Extension Service, grant 2005-35101-15344. Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA. The authors thank Carlos A. Masino and David Shockey as well as the graduate students from the Department of Animal Science of the University of Arkansas (Fayetteville) for their invaluable help during the sample collection period and analysis. The authors also acknowledge Michael H. Wade (Universidad Nacional del Centro de la Provincia de Buenos Aires, Argentina), Michael Phillips (Morehead State University, Morehead, KY), Rene Flores (University of Arkansas for Medical Sciences, Little Rock), and Hernando Flores (Corporacion Columbiana de Investigacion Agropecuaria, Bogota, Columbia) for their critical review, ideas, and comments to the manuscript.

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Received May 1, 2009.
Accepted July 29, 2009.

capture only those patterns and processes pertinent to their artificial conditions, which often make inferences difficult to apply on a larger scale (Wu, 1999). An example is the use of sward surface height for predicting difficult and variable ingestive behavior parameters such as bite mass. Using a microsward technique, Soder et al. (2009a) reported that sward surface height was the best predictor of bite mass. However, when the microsward technique was applied in different experimental conditions, Soder et al. (2009b) argued that bite mass was explained by leaf proportion of the canopy rather than by its height. Another example is the feeding station behavior of grazing ruminants under either artificial or field conditions. Although between 30 and 60 bites per feeding station has regularly been reported, such elevated values for individual feeding stations are rare in the field, where values average 10 bites per feeding station (Ruyle and Dwyer, 1985; Wade et al., 2006). In spite of these discrepancies, the foraging behavior concepts from such studies are being used to make informed grazing management decisions (Provenza, 2003). Therefore, studies integrating small-scale and artificially generated information with in-field pasture conditions are still lacking. The main objective of the present study was to describe the effects of different sward canopy structures on the short-term herbage intake rate and foraging dynamics of steers grazing wheat pastures.

MATERIALS AND METHODS

Animal procedures in the following experiments were conducted in accordance with recommendations of the Consortium (1999) and were approved by the University of Arkansas Institutional Animal Care and Use Committee.

Research Site, Pasture, and Treatments

The study was conducted at the University of Arkansas Agricultural Research and Extension Center, Fayetteville (36°18′ N, 94°16′ W), in March 2005. This study used wheat (*Triticum aestivum* L.) pastures planted as described by and for the purpose reported by Beck et al. (2008) in September 2004, using 3 tillage methods: conventional tillage (**CT**), minimum tillage (**MT**), and direct seeding (**NT**, no tillage). These pastures presented differential sward structures (as described below), which might or might not have been related to tillage method (measurements of sward canopy structure were not replicated in time, year, weather conditions or space, or their combination). Because of these differences, pastures were considered useful, and were thus used for the purpose and objective of the present study. For simplicity, treatments are named after the corresponding tillage methods. However, results and inferences do not refer to any particular or potential effect of the tillage method, but rather to the different sward canopy structures found. Pastures were not grazed previously until research was begun in March.

Animals and Experimental Setting

Three ruminally cannulated Angus steers (BW = 588 ± 28.3 kg) were presented to the 3 NT, MT, and CT pasture treatments. Treatments were presented by constructing 3 open grazing corridors within each pasture on the day before measurement. Each corridor was 18 m in length and 1.7 ± 0.2 m in width (Figure 1). The corridor width was set depending on the animal path width (Fortin et al., 2002; see Figure 1). Plastic posts were set every 2 m to facilitate observation and analysis. Grazing corridors were grazed (sampled) in grazing sessions (**GS**). A GS consisted of taking a steer (with rumen emptied 2 h before grazing the corridor) to the randomly allocated treatment and corridor, and letting it graze freely (unlimited time) until the end of the grazing corridor. The GS were videotaped from a distance of 2 m by recording transversely to the steer along the corridor to avoid angle errors during videotape analysis (Figure 1). After the steer finished the GS, it was immediately taken to the barn (30 m from the pastures) and ruminal contents were emptied, weighed, and sampled for DM. To avoid any disturbance in grazing behavior while steers grazed, each steer had its own camera operator, a person in charge of taking it to the grazing corridors, and 2 trained observers who counted bites and steps during the GS. Steers were fasted the night before and were fed 2 kg of ground corn grain (*Zea mays* L.) 3 h before the beginning of the GS to reduce differences in appetite, as described by Illius et al. (1995). Steers were adapted to the measurement team and trained to graze the grazing corridors in GS 1 mo before the measurement periods began. One week before this period, steers (with rumens evacuated) were grazing a corridor daily in the presence of the measurement team.

Measurements and Calculation

Treatment Characterization. To characterize each treatment, grazing corridors were sampled for undisturbed sward surface height, herbage mass, tiller density, and bulk density 1 d before the beginning of the GS. Herbage mass was determined at ground level by hand clipping nine 30-cm^2 quadrats in pasture sites adjacent to the corridors. Herbage samples were separated into leaves and stems, and leaves were classified and ranked in phenological order. Undisturbed sward surface heights were measured (pregrazing) at 60 random points in each corridor by using a sward stick (Barthram, 1986). Tiller density was measured in 3 fixed (corners and center) points of a grid quadrat (25 small quadrats of 15 cm^2). The grid quadrat was randomly thrown 3 times into pasture sites adjacent to the corridors. The undisturbed sward surface

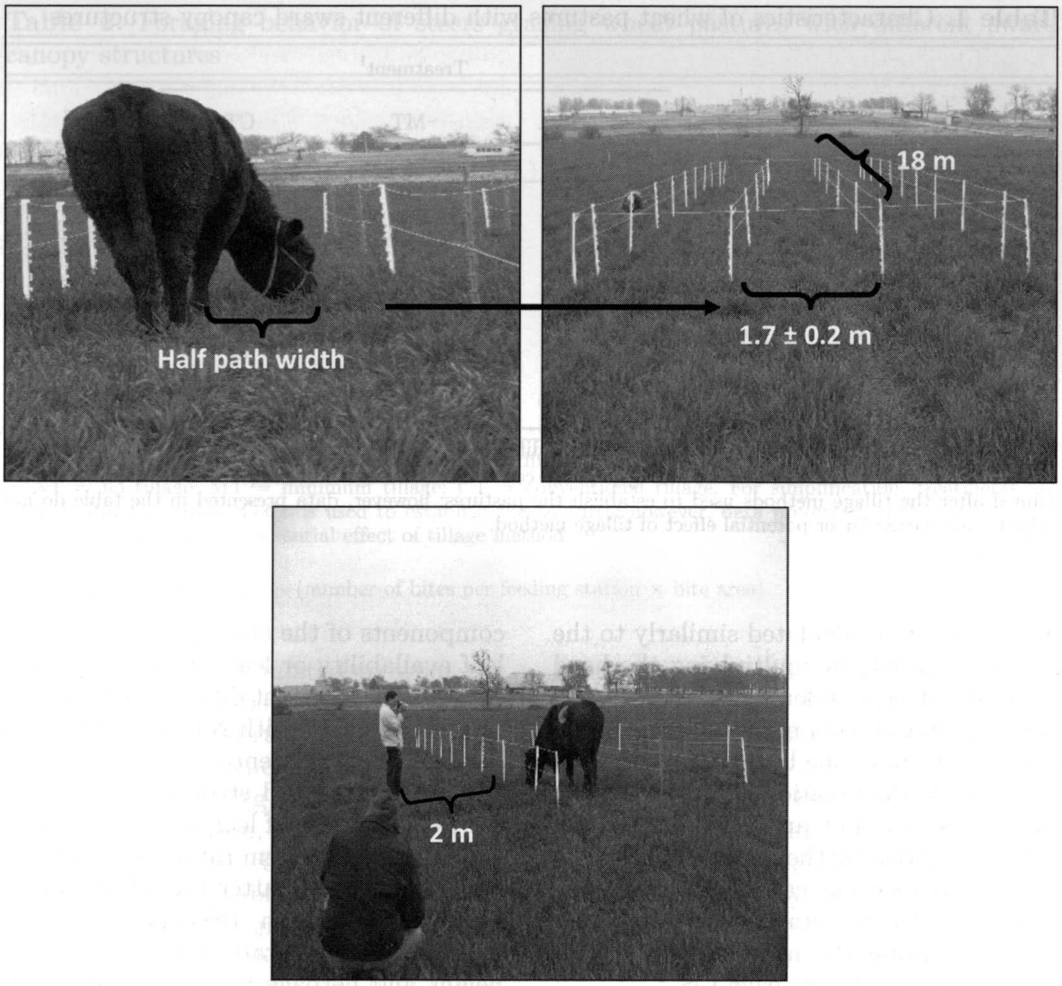

Figure 1. Grazing corridor dimensions and steer measurement team.

height (3 points) was also determined in each small quadrat, where herbage was cut to determine bulk density. Canopy was sampled for total biomass at 3 fixed strata: bottom, middle, and top. The fixed depth of each canopy stratum was one-third of the actual undisturbed sward surface height. The total biomass of each stratum was collected with modified scissors that did not allow the material to fall down (Griggs et al., 2005). The biomass from each stratum was separated into green and dead leaf and stem. The sampling procedure was the same for tiller density with the grid quadrat. Every sample, either total herbage mass or stratum biomass, was frozen (−20°C) immediately after sampling for further morphological analysis. After analysis of fresh weights, samples were oven-dried at 60°C for 48 h for DM determination. A pooled sample of total herbage mass was analyzed for OM, CP, NDF, ADF, and in vitro OM digestibility. The latter 3 analyses were conducted using the batch procedures outlined by Ankom Technology Corporation (Ankom Technology Corp., Macedon, NY). Concentrations of N in each sample were determined by rapid combustion (850°C), conversion of all N-combustion products to N_2, and subsequent measurement by a thermoconductivity cell (model FP-428, Leco Corp., St. Joseph, MI). Crude protein was calculated as the percentage of N in the sample multiplied by 6.25.

Herbage Intake and Foraging Behavior. Herbage intake rate was calculated as the herbage DM consumed at each GS (collected from the rumens after GS) divided by the total eating time (eating time = grazing time − searching time) of each GS. Bite mass was estimated by dividing the herbage intake by the number of bites during the GS. Bite depth was measured according to the method of Fortin et al. (2002). Fifteen measurements of extended tiller length were taken within every 2 m of the grazing corridors in grazed areas identified by the observers, and 15 more tillers were taken in immediately adjacent ungrazed areas. Bite mass, grazed stratum bulk density, and bite depth was used to calculate bite area according to the method of Laca et al. (1992). All videotapes were analyzed for eating time and the number of eating and searching steps. Each eating step was considered as a feeding station because with each eating step, steers defined a potential area of herbage consumption, as described by Ruyle and Dwyer (1985) and Rook et al. (2004). The eating step length was calculated by dividing 2 m of eating distance (using the plastic posts as a reference) by the number of eating steps taken in those 2 m. The

Table 1. Characteristics of wheat pastures with different sward canopy structures

	Treatment[1]			
Item	NT	MT	CT	SE[2]
Green leaf availability, g/m^2	280	275	279	32.7
Stem availability, g/m^2	213	200	177	30.4
Dead leaf availability, g/m^2	87.8	80.0	71.2	20.5
Bulk density, g/m^3	11,400	10,687	8,576	753.0
Tiller density, tiller/m^2	1,051	1,002	958	102.2
First leaf, g/m^2	88.7	83.4	48.2	20.69
Second leaf, g/m^2	107	80	114	14.8
Third leaf, g/m^2	74	68	68	11.4
Fourth leaf, g/m^2	9.1	9.7	6.3	1.51
Sward surface height, cm	23.6^b	20.4^a	19.5^a	0.54

^{a,b}Means within rows with uncommon superscripts differ ($P < 0.05$).

[1]NT = no tillage; MT = minimum tillage; CT = conventional tillage. For simplification, treatments are named after the tillage methods used to establish the pastures; however, data presented in the table do not refer to any particular or potential effect of tillage method.

[2]n = 9.

area of a feeding station was calculated similarly to the method of Rook et al. (2004) by multiplying the head sweep times the mean eating step length. Therefore, the calculated area per feeding station minus the number of bites per feeding station times the bite area resulted in the area consumed per feeding station—in other words, the evenness of grazing per unit area. The number of bites of every GS was divided by the eating time, and in doing so, the eating bite rate was calculated. The average number of bites per feeding station was calculated (video analysis) by counting the number of bites per eating step (feeding station) during each GS.

Statistical Analysis. Dependent variables were analyzed by ANOVA as a 3 × 3 Latin square (Kuehl, 1999), using a GLM (SAS Inst. Inc., Cary, NC). The experimental unit was the corridor per steer (each steer went through the 3 treatments). The model used to analyze canopy stratum variables included the fixed effects of canopy stratum, treatment, and the interaction of canopy stratum × treatment. The model used to analyze foraging behavior variables included the fixed effects of grazing corridor per steer, treatment, and the interaction of grazing corridor per steer × treatment. When the F-test was significant ($P < 0.05$), least squares means were separated using the predicted differences option within the GLM procedure in SAS.

RESULTS AND DISCUSSION

Under the conditions of this experiment, herbage mass did not differ ($P > 0.05$) between treatments when green and dead leaf availability and stem availability were considered (Table 1). Herbage chemical composition was similar between treatments (90.5 ± 2.01 OM, 22.6 ± 2.28 CP, 37.4 ± 2.44 NDF, 38.6 ± 3.24 ADF, and 90.1 ± 0.57 in vitro OM digestibility; averaged as percentage of DM). Tiller density did not differ ($P = 0.87$) between treatments, implying a potentially greater weight per tiller for NT. In contrast, there were no differences ($P > 0.05$) in morphological components of the canopy, even when comparing green leaf availability or leaf phenological ranking (Table 1). Sward surface height differed ($P < 0.05$) between treatments (Table 1), with NT being the tallest ($P < 0.05$). Hence, when the entire canopy was considered, the steers grazed sward structures of similar quality, with the same amount of leaf, the same amount of stem, and the same leaf-to-stem ratio, but different sward surface heights, with the latter probably affecting herbage accessibility (Hodgson, 1981; Laca et al., 1992).

Herbage intake rate is influenced by sward surface height and herbage weight per unit of canopy volume (Black and Kenney, 1984; Gibb et al., 1997). The question is whether the present difference in sward surface height between treatments can explain the magnitude of difference in herbage intake rates and the associated foraging behavior (Table 2). Under NT, steers had an herbage intake rate 1.9 times greater ($P < 0.05$) than when grazing MT or CT.

Structural heterogeneity in plants arises from variation in the way plant tissue is arrayed in space, which leads to different canopy architectures. These variations affect feed intake by mammalian herbivores (Hobbs et al., 2003). Hence, mean values of biomass or sward surface height would be poor predictors of cattle foraging behavior responses (Laca et al., 1992; Bergman et al., 2000, 2001) and, consequently, herbage intake. In the present study, the different treatments did not differ ($P > 0.05$) in leaf biomass (green or dead) at any canopy stratum (Table 3). However, there was a clear difference ($P < 0.01$) in the vertical arrangement (distribution across the sward canopy) in all the variables analyzed (Table 3). The mean biomass distribution was 76, 17, and 6.8% for the bottom, middle, and top strata, respectively. This distribution follows a pyramidal biomass distribution, which might be expected for any winter annual grass (Galli, 1994). The canopy stratum depth was determined by the sward surface height and not by the potential bite depth. This allowed sward and animal measurements to be retained independently and

Table 2. Foraging behavior of steers grazing wheat pastures with different sward canopy structures

Item	Treatment[1] NT	MT	CT	SE[2]
Herbage intake rate, g/min	146.3[a]	64.8[b]	88.9[b]	21.27
Eating bite rate, bite/min	49	52	46	4.21
Bite mass, g	2.9[a]	1.3[b]	1.9[b]	0.30
Bite depth, % of extended tiller length	55	56	55	0.1
Bite area, cm^2	118[a]	65[b]	83[b]	9.7
Feeding stations	18[b]	48[a]	29[c]	5.7
Bites per feeding station	12	12	13	2.4
Feeding stations/min	2.6[b]	4.2[a]	3.5[b]	0.49
Area consumed at each feeding station,[3] %	87[a]	31[b]	38[b]	0.1

[a–c]Means within rows with uncommon superscripts differ ($P < 0.05$).

[1]NT = no tillage; MT = minimum tillage; CT = conventional tillage. For simplification, treatments are named after the tillage methods used to establish the pastures; however, data presented in the table do not refer to any particular or potential effect of tillage method.

[2]n = 3.

[3]Area per feeding station − (number of bites per feeding station × bite area).

foraging behavior variables to be related to what the animal was grazing (M. J. Gibb, Institute of Grasslands and Environmental Research, North Wyke, UK; personal communication). Despite the lack of treatment differences ($P > 0.05$) in amount (g/m^2) of leaf or stem available in every canopy stratum, there was a strong interaction ($P < 0.05$) between canopy stratum and treatment in leaf proportion (Table 3). This interaction means that the canopy strata presented a different array of morphological organs to the grazing steers depending on treatment. The NT treatment offered more ($P < 0.01$) leaves in the middle and top strata than did the MT or CT treatment. This increase and the difference mentioned in sward surface height could have synergistically influenced the foraging behavior of steers because the herbage intake rate is a function not only of the amount herbage available, but also of plant characteristics determining herbage accessibility (Spalinger and Hobbs, 1992; Drescher, 2003).

Generally, ruminants remove only the uppermost parts of the plants, which may be an active mechanism imposed by the physical structure of plant tissues to overcome resistance to defoliation (Illius et al., 1995; Griffiths and Gordon, 2003). As mentioned, NT presented the greatest sward surface height and the greater leaf proportion in the upper strata (top and middle). In fact, the top stratum was all leaf material (Table 3). Therefore, because of the bendable feature of leaf tissue, muzzle insertion within those NT strata would be easier than for insertion within the MT or CT strata. This would be reinforced by the concept of bite force-plant resistance information proposed by Griffiths and Gordon (2003). Consequently, deeper bites would be expected for NT, helping to explain the greater bite volume (bite volume = actual bite depth × bite area), and therefore herbage intake rate, through a greater bite mass. Although, bite depth as a percentage of extended tiller length was basically the same between treatments ($P > 0.05$; Table 2), the combination of this percentage and the sward surface height indicates that the actual bite depth in NT was the greatest. This means that sward surface height and factors related to muzzle penetration (i.e., leaf proportion in the canopy strata) could have been involved in the potential differences in bite shape, bite mass, and, consequently, herbage intake rate. The effect of such associative factors is supported by previous research by Wade et al. (1989, 1995), who reported a proportional relationship between bite depth and sward surface height, and an increase in herbage accessibility with the proportion of leaf. The latter matches previous reports by Weddell et al. (1997) and Hazard et al. (1998), who demonstrated the importance of plant leafiness for intake by ruminants.

Stems may act as a barrier to bite depth in short and dense swards (Flores et al., 1993; Hongo, 1998), which was not the case for the swards in the present study. However, in a horizontal dimension, stems might have affected bite formation and shape. Stems could be an obstacle to tongue sweeping and could therefore reduce the bite area, and thus the bite mass (Benvenutti et al., 2006). This concept was demonstrated by the reduction in bite mass reported by Prache (1997), who evaluated the impact of reproductive stems on bite characteristics and herbage intake rate. Bite area differed ($P < 0.05$) between treatments (Table 2) and was greatest in NT. It follows, based on an optimal foraging theory, that the greater proportion of accessible leaves could have improved the ability of steers to take bites from a larger area in the upper strata of NT.

The question remains regarding how grazing ruminants perceive and then react in the horizontal dimension to swards offering strata with the same herbage availability but with differences in morphological component ratios (herbage accessibility). The short-term profitability of plants as a food source for herbivores is defined as DE per unit of handling time (Fortin, 2001). Burns et al. (1991), who compared the top and bottom

Table 3. Canopy strata characteristics (top, middle, bottom) of wheat pastures with different sward canopy structures[1]

Item	NT			MT			CT			SE[2]	P-value		
	Top	Middle	Bottom	Top	Middle	Bottom	Top	Middle	Bottom		Treatment	Canopy strata	Treatment × canopy strata
Total weight, g/m^2	11.9	37.0	173.2	11.6	35.2	171.5	18.5	33.7	127.5	13.86	0.72	<0.01	0.78
DM, %	23	21	19	16	23	21	20	19	18	0.01	0.59	0.55	0.14
Green leaf, g/m^2	11.9	31.9	45.2	11.5	28.1	29.6	18.5	23.9	30.2	3.32	0.32	<0.01	0.37
Dead leaf, g/m^2	0	0	32.4	0	0.7	22.1	0	0.07	20.8	2.71	0.56	<0.01	0.64
Stem, g/m^2	0	3.5	63.9	0.1	4.4	41.8	0	5.0	34.0	4.7	0.33	<0.01	0.28
Total leaf dry, g/m^2	12.0	31.9	77.7	11.5	28.8	51.8	18.5	24.0	51.0	5.24	0.33	<0.01	0.40
Leaf content, %	100^c	86^c	26^c	99^c	80^b	17^b	100^a	71^a	24^b	2.1	0.14	<0.01	0.02

$^{a–c}$Least squares means within rows and strata with uncommon superscripts differ ($P < 0.05$).

[1]NT = no tillage; MT = minimum tillage; CT = conventional tillage. For simplification, treatments are named after the tillage methods used to establish the pastures; however, data presented in the table do not refer to any particular or potential effect of tillage method.

[2]n = 9.

strata of several grasses, suggested that plant part proportions among canopy strata are key determinants of herbage in vitro DM digestibility. This raises the question of whether NT swards would lead to more profitable (as defined by Fortin, 2001) bite and feeding stations. Neither area nor time restrictions were imposed during the GS. Steers were allowed to manage their GS time and behavior while moving through the corridor. The number of feeding stations and the velocity of eating (feeding stations per minute) was least with NT ($P < 0.05$). The latter indicates that residence time per feeding station (the inverse of feeding stations per minute) was the greatest in NT (Table 2). The heavier bites taken at each feeding station in the NT treatment may have led to increases in manipulative movements (Laca et al., 1991; Hodgson et al., 1997) and, consequently, to the necessity of investing more time at each feeding station. The number of bites per feeding station did not differ between treatments ($P > 0.05$), which agrees with the results of Forbes and Coleman (1993), who found little effect of canopy structure and mass on bite rate. In the feeding stations of MT and CT, each bite seemed to be either less profitable or harder to take. Otherwise, steers may have taken more bites per feeding station. Steers in the MT and CT treatments moved more rapidly during the GS, which was demonstrated by the greater ($P < 0.05$) number of feeding stations. The number of feeding stations per minute in MT could indicate a greater necessity to move on and search for more profitable bites or feeding stations. It is still unclear whether the steers were seeking leaves and whether MT and CT had less profitable feeding stations.

In NT, such a necessity of moving on and searching for more leaves seemed to be reduced, making the animals more static and slower, but more efficient. The latter was visually demonstrated ($P < 0.05$) by the percentage of area grazed per feeding station among treatments (Table 2). According to Shipley et al. (1996), if an animal must slow down and stop to select a bite, this increases its foraging time and the energy expended to overcome inertia when it leaves the plant; thus, the animal may choose to exploit many bites at one feeding station before moving on. This would be logical and would match the results of the present study, although the number of bites per feeding station did not differ among treatments ($P > 0.05$). In NT, it was apparently more beneficial for steers to stop and spend more time per feeding station, using most of them rather than to keep moving without losing inertia. When steers grazed MT or CT, they seemed to try to compensate for the smaller bites by making the dynamics of grazing energetically more efficient. This premise is supported by the reports of WallisDeVries et al. (1999), who argued that the greatest potential for selection appeared to exist in the choice of feeding stations, and Hongo (1998), who pointed out that site selection (feeding station, in this case) is closely related to heterogeneity of vegetation. In relation to these works, the results of the present study may also present a picture of how vertical heterogeneity relates to the horizontal dimension of grazing dynamics, even in monoculture pastures. Under field conditions, Stobbs (1973) reported a positive correlation between bite mass and leaf percentage in the upper strata (r = 0.73), and Hendricksen and Minson (1980) reported r = 0.81 when relating the BM and the leaf-to-stem ratio. Animals choose to seek out and avoid foods and parts of foods. In the present study, steers seemed to seek out more profitable (leafy) bites or sites (feeding stations), or both.

In summary, pastures with greater leaf accessibility and similar herbage quality may lead grazing cattle to reach the same herbage intake amount in less time while possibly grazing more efficiently per unit area. Consequently, when cattle are grazed by using intermittent defoliation methods, it would be logical to think of reducing the area and time allocation in pastures where taller swards with leafy upper canopy strata are found.

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